

BEHAVIORAL ASPECTS OF THE PAIR BOND IN WILSON'S PHALAROPE

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Sex role reversal, in which females take the active role in pair formation and the smaller and more cryptically colored males take sole responsibility for incubation and parental care, is typical of all species of phalaropes (Bent 1927, Tinbergen 1935, Höhn 1965, 1967, Bengtson 1968, Hilden and Vuolanto 1972). In at least one species, the Northern Phalarope (*Phalaropus lobatus*), sex role reversal occurs in conjunction with serial polyandry, a system in which females form short-term pair bonds with at least 2 successive males (Raner 1972, Hilden and Vuolanto 1972). The behavioral mechanisms which enable species with sex role reversal to achieve effective integration of male and female roles, leading to formation of a pair bond and successful breeding, have not been examined in detail.

Howe (1975) discussed the social phase of early pair formation in flocks of Wilson's Phalaropes (*Phalaropus tricolor*) in North Dakota. The social phase takes place during the last week of April and the first half of May. At this time the birds confine most activity to open water of ponds and lakes and to segments of shoreline unobstructed by vegetation. Aggression among females competing for males manifests itself in both overt and ritualized form in swimming groups and during aerial pursuits. One immediate result of these interactions in both contexts is a reduction of competition among females for mates, either by increasing interfemale distances or by decreasing the number of females present.

Reduced competition among females leads to greater opportunity for direct interaction between a female and her potential mate. During the early stages of pair formation such interactions consist primarily of persistent attention and cautious approach by the female and occasional threat by the male. The female also performs an epigamic display, "Chugging," which often elicits male threat. As the male of a forming pair becomes more tolerant of the courting female, the birds spend more time apart from conspecifics and new behavior patterns begin to emerge. The present paper deals with this phase of pair formation in Wilson's Phalarope and examines the roles of the sexes in the pair bond. This period includes investigation of potential nesting areas, territoriality, nest-building, copulatory behavior, egg-laying, and certain other behavior patterns restricted to paired birds. The behavior of females after laying and its implications are also considered.

STUDY AREA AND METHODS

The observations reported here were made in May and June of 1969 and 1970 and in May of 1971 near Woodworth, Stutsman Co., North Dakota. The area, described in more detail elsewhere (Howe 1975), consists of rolling, highly disturbed, mixed-grass prairie with numerous small potholes of glacial origin. Phalaropes use the potholes for feeding and nest on the ground on the periphery of the potholes or on nearby higher ground. Most behavior observations were made in an area of approximately 1 km² which supported an average nesting population of 7 males.

Phalaropes were usually watched from an automobile or conventional portable blind. Durations of behavioral events were determined by stopwatch and, in certain cases, by recording the playback time of taped field notes. Most observations of behavior before egg-laying were made on unmarked birds. Three females and 2 males, however, were trapped during the egg-laying period with a spring-loaded bale trap anchored at the edge of the nest. These birds were marked with colored leg bands and diagnostic dye patterns on the plumage and released immediately.

Ten females were collected and examined for evidence of post-ovulatory follicles. In addition to gross examination, all ovaries were fixed, sectioned at 1 mm intervals, and stained, following the staining technique of Erpino (1969). This method of locating post-ovulatory follicles has been used successfully by Payne (1966) and Parmelee and Payne (1973).

In this paper the names of vocalizations and other behavior patterns which appear to be ritualized are capitalized, e.g. Pre-Copulatory Bow.

INVESTIGATION OF NESTING AREAS

By the third week of May most activity of courting groups of phalaropes had shifted from the central portions of large bodies of water to shallow water near shore and to smaller sloughs in which new growth of sedge (*Carex* spp.) was beginning to emerge. Although this was the peak period of aerial chasing activity, males were now better able to elude pursuing females by landing in vegetated sloughs and swimming into the vegetation. In such areas forming pairs were able to avoid detection by conspecifics for longer periods of time. In the absence of interference from other birds, potential mates began investigating drier grassy areas where nests would ultimately be placed.

Early ventures into grassy areas were nearly always initiated by the female (Table 1a). In about half of my observations the male did not follow and the female returned to the shore. Six cases in which unpaired females attempted to lead known paired males away from the shore elicited either threat by the male or no response at all.

When either a male or female left the shore and entered the grass the "crouch walk" posture was generally used (Fig. 1a). In this posture the neck was withdrawn, the body was tilted forward with the head slightly below the level of the tips of the wings and tail, and the back feathers were sometimes ruffled. Crouch-walking reduced a bird's conspicuousness in the grass and,

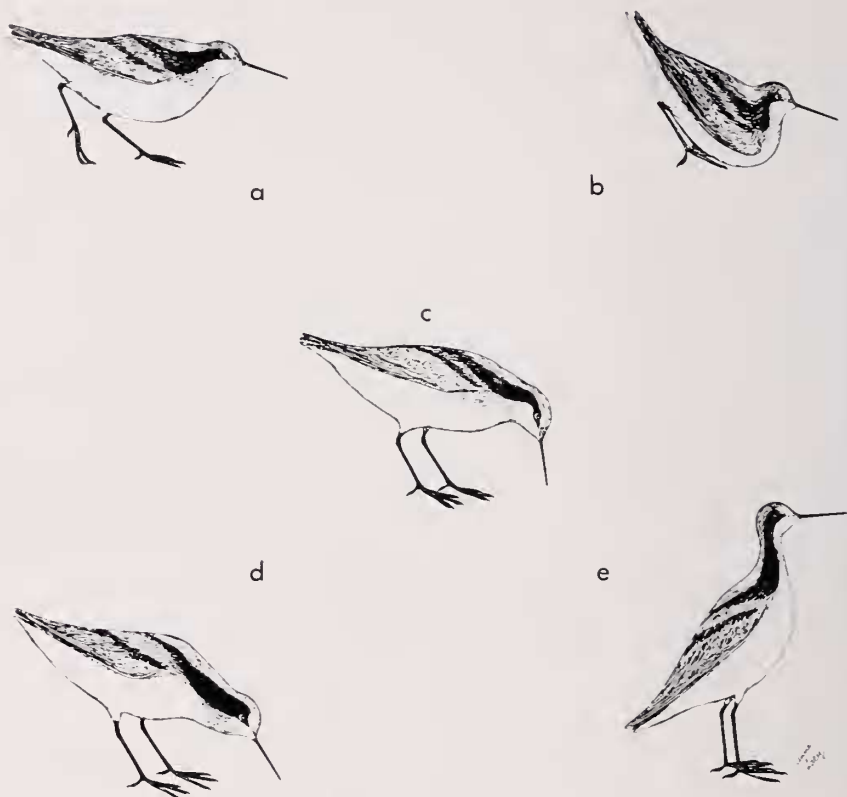


FIG. 1. Postures and displays associated with nest-area exploration, nest-construction and copulation: (a) Crouch-walk; (b) Pre-Copulatory Bow (PCB) Type I, also Scraping; (c) PCB Type II, also Ground-Pecking; (d) PCB Type III; (e) Pre-Copulatory Upright (PCU).

since the head was close to the ground surface, it probably facilitated close examination of potential nest locations. The position of the tail exposed the white undertail coverts to the following bird and may have been of significance in eliciting a following response.

The behavior of females after entering the grass could not be seen in many instances. Several times, however, I observed females adopt a form of the "Pre-Copulatory Bow" (PCB) posture (Fig. 1b, c, d) about 3 to 6 m from the shore. If the male was not already following the female, he usually ran toward her while she was performing the display, possibly in response to a vocalization rather than the posture per se. Sometimes this response led to fragmentary pre-copulatory behavior by both birds and at other times it led to nest-site searching. Copulatory and nest-site searching tendencies were

TABLE 1
MALE-FEMALE INTERACTIONS DURING THE PERIOD OF NEST-SITE SEARCHING

A. Relative positions while Crouch-Walking

| | Sex Initiating Sequence | Sex Leading During Sequence |
|--------|-------------------------|-----------------------------|
| Female | 27 ¹ | 28 |
| Male | 3 | 30 |

B. Role in scrape ceremonies

| Female Only | Male Only | Female Followed by Male | Male Followed by Female |
|-----------------|-----------|-------------------------|-------------------------|
| 15 ¹ | 21 | 8 | 8 |

¹ Number of observations

occasionally expressed ambivalently. As a result it was often difficult to interpret the motivational basis of the behavior in these situations. Pre-dominance of copulatory tendency was apparent in females which entered the grass with the neck extended vertically, a posture suggesting the "Pre-Copulatory Upright" (PCU) display (Fig. 1e). The complicated relationships between precopulatory and nest-site searching behavior are discussed further under "Copulatory Behavior."

Most early expressions of nest-site searching behavior that I observed began with a female and male walking out into the grass from a slough. Sometimes 2 birds would fly from a slough and land in dry grass some distance from the water, but these birds may have been ones which had already selected a potential nesting area. In mid-May old grass was generally less than 12 cm high in the areas selected except in occasional clumps. Early nesters began nest-site searching before new grass had emerged. Typically the 2 moved through the grass in the crouch-walk posture, one following the other or both wandering in separate directions and eventually rejoining. Usually visual contact was maintained but vocal communication also played an important role. Much of nest-site searching in this species was difficult to observe because the birds were often concealed by grass: but the instances observed (Table 1a) show that either sex may play a leading role once both are away from the shoreline.

Periodically during crouch-walking sequences, one sex or the other crouched in the grass and performed "Scraping" behavior. In this posture the bill was directed forward and down, the tail was raised almost vertically, and the tarsi were pushed backward against the wall of the shallow depression (or "scrape") that was formed (Fig. 1b). Sometimes the performing bird turned

around slowly in the depression. This was the same behavior performed later by males to form the cup at the nest, but at this early stage of the nesting cycle it appeared to be ritualized. It usually lasted for a few seconds and then the bird continued in a crouch-walk. Often the second member of the pair approached the Scraping bird from the rear and bowed forward in a posture similar to the first. This sometimes was followed by "Ground-Pecking," a display in which one or both birds pecked sporadically at the ground or grass in a stereotyped posture (Fig. 1c) similar to that of an uncommon form of the PCB. At this point the first bird may leave the depression while the second enters and Scrapes. Ritualized Scraping during pair formation was first given the name "Scrape Ceremony" by Huxley and Montague (1926), who observed it in the Black-tailed Godwit (*Limosa limosa*). Scrape Ceremonies have been reported for many ground-nesting birds particularly in the Charadrii and Laridae, occurring either in nest-site selection or precopulatory situations. Tinbergen's (1935) detailed account for the Northern Phalarope agrees closely with my observations of Wilson's Phalarope.

Although Scrape Ceremonies involved ritualized behavior patterns, the sequence of events was variable. Scraping by one bird did not necessarily elicit Scraping by the other, and often one sex Scraped while the other was too distant to observe. Often simultaneous Scraping by both occurred without Ground-Pecking. In one instance 2 birds Scraped simultaneously in the same spot while facing each other: then the female left and the male remained and turned slowly in the scrape for 10 sec after which the female returned and entered the scrape again.

Ground-Pecking often occurred when one sex replaced the other at a scrape. It was usually directed into the scrape itself and might be performed by both birds at the same time, closely resembling the "Egg Ceremony" of the Northern Phalarope (Tinbergen 1935). The performance of Ground-Pecking along with a Scrape Ceremony may be a mechanism for designating the most favorable potential nest locations. Ultimately the male alone denudes several scrapes by pulling up grass and rootlets. One of these scrapes becomes the nest, but the means by which the actual site is selected is not clear. A series of Scrape Ceremonies may last 2 hours or more at dozens of sites and cover distances up to 100 m.

Fifty-two instances of Scraping were noted (Table 1b). Either sex was equally likely to lead the other in mutual ceremonies and both males and females sometimes Scraped separately.

PREPARATION OF THE NEST SCRAPES

One or 2 days before the laying of the first egg, nest-site searching ceased. The male returned to several of the depressions previously formed by Scrap-

ing (scrapes) and began to pull up dead grass and fresh grass if present. The position of the body while pulling grass strongly suggested Ground-Pecking and is likely the behavior from which that display is derived. After several hours at each scrape, circular areas about 10 cm in diameter were denuded except for the larger rootlets. Scrapes were considered complete when denuded to a diameter of 10 cm, this being the average diameter of nests. Sometimes the male divided his activity among several different sites before completing any. Typically 2 or 3 were completed and several were left incomplete. One male repeatedly visited 6 or 7, performing scraping behavior in all of them and removing grass in several. After 2 hours, 2 of the scrapes had been denuded to diameters of 5 cm. In this particular case all of the scrapes visited were within 7 m of one another. In 2 other instances, however, scrapes denuded by a single male were nearly 30 m apart.

Höhn (1967) felt that the female Wilson's Phalarope was primarily responsible for denuding scrapes, but I found no evidence of direct participation by females. My observations at 6 nests from nest scrape preparation through egg-laying indicated that only males prepared the scrapes, although the females performed occasional Ground-Pecking behavior during Scrape Ceremonies and sometimes visited their mates while they were preparing scrapes. In the Red Phalarope (*Phalaropus fulicarius*), apparently only the male prepares and builds the nest as well (H. Mayfield, pers. comm.). It is not known, however, if Red or Northern phalaropes denude the nest scrape before the first egg is laid.

TERRITORIAL BEHAVIOR

Male territorial behavior was observed only once during the nest scrape preparation period. On 27 May 1970 a lone male was active at several scrapes when a pair began nest-site searching in the same area. As they passed within 3 m of the male, he crouched low for several seconds, directed a "Flying Threat" (see Howe 1975, for threat descriptions) at the male of the pair, and then gave several Flying Threats and "Head Forward Threats" to the female. Over a period of 2 hours the first male gave several Flying Threats and overt attacks, most of which were directed at the female of the pair although she had directed no displays toward him. The female responded to the attacks with several "Bill-Downs" (BD, see below), a display probably serving an appeasement function. The pair remained in the area despite the frequent attacks, which continued even after the pair had moved 25 m away from the area where the first male was clearing nest scrapes. Finally the male flew in and hovered over the female of the pair and gave the "Ernt" call characteristic of aerial chases (see Howe 1975). The pair and a second female joined the male in a short aerial chase which ended in the nearest slough. This was clearly an attempt by a male to defend a small area

around the nest scrapes he was preparing. I observed no other case of direct competition for a nesting area.

After the onset of incubation, a male did not actively defend the nest area unless an unpaired female followed him back to the immediate vicinity of the nest. Since I found active nests as close as 5 m apart, any territorial tendency present during nest scrape preparation was apparently lost by the time incubation began. Nests of the Northern Phalarope have been found 1 pace (Selous 1915) and 5 paces (Höhn 1971) apart; 2 nests of the Red Phalarope were found 7 paces apart (Rüppell 1968). These observations suggest that males of all species of phalaropes do not exhibit strong territorial behavior, if any, during incubation. However, the males in question could have been mated to the same female.

Females were territorial in the sense that they defended the mobile positions of males during the courtship period, but only twice did I observe females exhibiting behavior which might have represented defense of a breeding area. In each case a swimming female threatened another with Flying Threats in the apparent absence of any males. I could not be absolutely certain that no males were present, however, and the possibility of feeding competition in these isolated instances could not be ruled out. Therefore I have not recorded any definite examples of females exhibiting territorial behavior related to a breeding area. This conclusion agrees with that of Höhn (1967) for Wilson's Phalarope. Tinbergen (1935) presented evidence suggestive of territorial behavior in breeding female Northern Phalaropes but Höhn (1971) was unable to corroborate these observations. Neither Höhn (1971) nor Bengtson (1968) felt that the Red Phalarope exhibits territorial behavior although the function of female "circle-flights" observed by the latter is not clear.

COPULATORY BEHAVIOR

Successful copulations probably occurred mainly in well-established pairs but unsuccessful attempts often took place in the early stages of pair formation. Either sex initiated a copulatory sequence, which sometimes included several highly ritualized precopulatory displays. Copulations took place while the birds were standing in shallow water or on shores of sloughs. Only 1 of 51 copulations or copulation attempts I observed took place between birds swimming in deep water. My observations conform to those of Höhn (1967) but differ strikingly from those of Johns (1969), who recorded 37 swimming copulations of a total of 53 observed over a 5-year period. According to Johns (pers. comm.), the bodies of water on his Montana and Washington study areas had an abundance of shoreline suitable for standing copulations, so it is difficult to explain why swimming copulations were so

frequent. Possibly Johns misinterpreted some overt attacks on females by males as copulation attempts, since he noted that "in these cases the male lit on the swimming female's back and pecked lightly at the top of her head for the 2 to 4 seconds of the act" (Johns 1969:665). I rarely observed head-pecking except during attacks and most copulations I observed lasted longer than 2 to 4 sec (see below).

Some of the pre-copulatory displays of Wilson's Phalarope have been described and illustrated by Höhn (1967). He concluded that behavior associated with copulation varies greatly but that a complete sequence includes the "Head-Up" and "Head-Down" postures. He observed one Head-Up posture (in a male), which he described as a rigid pose with the neck extended vertically and the bill pointed upwards at a 45° angle. In observations of 51 copulations I recorded this posture only once and it was performed by a female.

More frequent was the posture I call the "Pre-Copulatory Upright" (PCU, Fig. 1e). The PCU posture by the male preceded every mount I observed and was probably what Höhn (1967) described for one copulation as a "partially erect pose." In PCU the bird stood erect with the neck extended vertically but, unlike Höhn's Head-Up, the bill was directed forward. A male in the PCU posture made many rapid treading movements slightly forward, backward or sideways. The head remained more stationary than the rest of the body and consequently the neck and body appeared to sway back and forth. Orientation with respect to the female was variable. Sometimes the sequence ended at this point: otherwise the male moved around to the rear of the female and attempted to mount. PCU was usually performed simultaneously by both sexes but the female's neck was often partially dilated suggesting that the *Chug* call (see Howe 1975) was being given. In one case 2 birds faced each other in PCU pecking lightly at each other's bills before the male moved around to mount. PCU occurred almost simultaneously in both sexes but, in 6 cases observed under especially favorable conditions, the female initiated 5.

The PCU was often the only obvious pre-copulatory display. The forward and backward treading movements suggested expression of conflicting tendencies to approach and withdraw. The extended neck (resembling a pre-flight posture) and occasional running away (usually by the female) while maintaining the PCU posture suggested the predominance of a withdrawal tendency. The extended neck might be a prolonged and partially ritualized pre-flight posture. The PCU was typically held for 3 to 10 sec.

The Head-Down pre-copulatory posture, observed by Höhn (1967) in both sexes, sometimes occurred as a preliminary to PCU. However other postures with a lowered head were also used and the relationships between these pos-

tures are confusing. Because of the difficulty of distinguishing among them I have grouped them under the term "Pre-Copulatory Bow" (PCB). The form described by Höhn (1967) (PCB Type II, Fig. 1c) is apparently the rarest. More common is a posture similar to scraping (PCB Type I, Fig. 1b). Both are rigidly maintained but at least one intermediate between them occurs (PCB Type III, Fig. 1d). The PCB might better be interpreted as a continuum of display postures reflecting varying strengths of tendency to copulate. These displays last for only a few seconds, but once I observed a female maintain the posture for 15 sec. A similar-appearing display, the Bill-Down (BD), also occurred in pre-copulatory situations but probably has a different motivational basis and evolutionary origin (see below).

Many similarities exist between some pre-copulatory behavior and the behavior of pairs engaged in nest-site searching. PCB Type I is similar to a bird Scraping in a nest cup. PCB Type II closely resembles Ground-Pecking. Both forms were often given by females early in pair formation after attempting to lead a male away from the shore. The temporal overlap of copulatory and nest-site searching behavior during the breeding cycle led to situations in which tendencies toward each were present at the same time. It is not surprising, then, that pre-copulatory displays of Wilson's Phalarope appear to have been in part derived from behaviors directly related to nesting.

A female epigamic display, "Chugging," was frequently used during the courtship period (Howe 1975). In this display the neck is extended vertically, the throat dilated and a repetitive, low-pitched, frog-like call given. As pointed out above, the same call was possibly given during the PCU display. Chugging was also given by females at the beginning of about 25% of the copulatory sequences (usually incomplete) I observed. In an established pair Chugging did not elicit an aggressive reaction on the part of the male as it often did during social courtship. When members of a pair were not both sufficiently motivated for copulation, a series of Chugging, PCB's, PCU's and BD's (see below) might go on sporadically for several minutes without copulation being attempted. Chugging may have occurred more frequently in pre-copulatory situations than I have recorded, since the call is faint and difficult to hear.

No other pre-copulatory displays were observed. Particularly striking was the absence of wing-quivering with the wings held high over the back, a pre-copulatory display characteristic of many tringine sandpipers, the closest relatives of phalaropes (Jehl 1968). There were no post-copulatory displays. Behavior following copulation was variable but most often the pair flew away with the female in the lead. These flights are discussed in detail below (see "Pair Flights").

Seven complete copulations timed from the onset of pre-copulatory behavior

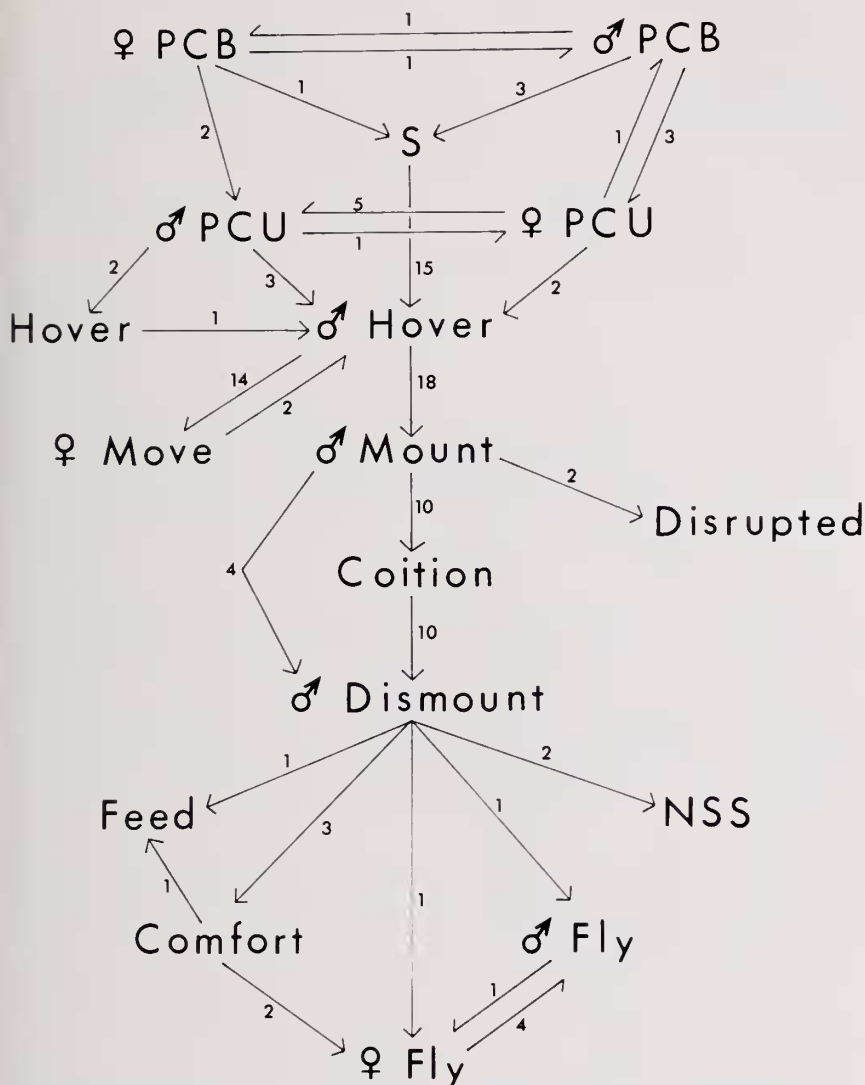


FIG. 2. Flow diagram of behavior sequences during 34 complete or incomplete copulations observed from the onset of pre-copulatory behavior. "Chugging" (see text) is not included. PCB = Pre-Copulatory Bow. PCU = Pre-Copulatory Upright. S = Virtually simultaneous PCU by both sexes. NSS = Nest-site searching.

(excluding Chugging) to the dismount averaged 46.5 sec with a range of 27 to 68 sec. A flow chart of copulatory behavior is presented in Fig. 2. The frequency of copulations is not known, although one pair copulated twice within 85 min.

OTHER BEHAVIOR PATTERNS OF PAIRING AND PAIRED BIRDS

Hostility existed between members of the forming pair, even during the early stages of nest-site searching. The male often showed intolerance of the female when she was closer than .5 m and mutual Scrape Ceremonies were occasionally interrupted momentarily by male threat. Hostility between the members of the pair gradually disappeared during the nest-site searching period. Several behavior patterns, in addition to Scraping, seemed to function in part as hostility-reducing mechanisms:

Preening.—A normal period of preening in unpaired, migrating Wilson's Phalaropes lasted about 8 to 10 min. but 2 pairing birds often spent up to 25 min preening as they stood only several cm apart. While preening the birds usually faced in the same direction but occasionally they would face one another without showing hostility. In other contexts facing at close range was rarely tolerated. Similar prolonged and possibly ritualized preening occurs in many avian species during and after pair formation and may facilitate adjustment of one sex to the close presence of the other. Allopreening was never observed.

Bill-down (BD) displays.—These displays were observed 29 times in females and 5 times in males. The form of the BD was variable; the 2 extremes are illustrated in Figure 3a and b. Of the 34 records, 16 occurred prior to precopulatory sequences, 5 during periods of nest-site selection and 13 when a male and female were simply in close proximity and facing each other. All were given while facing the mate at a distance of 1 m or less. BD's lasted only for a fraction of a second but sometimes were repeated 3 or 4 times in rapid succession.

Two observations suggest that BD's had an appeasement function. In each case the female of a pair flew in to join her mate, eliciting a Head Forward Threat from the latter. The female immediately responded with BD's and male aggression ceased. BD's presumably minimize the threatening potential of the bill. Since all observations of BD's involved birds close together in later stages of pair formation, it is likely that the display served to reduce aggressive tendencies in the mate, permitting the 2 birds to remain close to each other. The display appeared to be almost identical to precopulatory "Pushing" in Red Phalaropes (Bengtson 1968, Andrew 1955) except that in Pushing the female actually comes into contact with the male.

BD displays of the Type I variety (Fig. 3a) resembled normal breast preening but were easily distinguished in being very brief and regularly rhythmic when several were given in succession. It seems likely that these displays have been ritualized from preening behavior. On 5 occasions I observed birds perform apparent displacement preening of the breast during precopulatory



FIG. 3. Bill-Down Displays: a. Type I; b. Type II.

behavior or Scrape Ceremonies. Each case involved a male and female in close proximity, a situation in which BD's could be expected to occur. The form of BD Type II (Fig. 3b) was reminiscent of belly-preening but also resembled PCB Type II (Fig. 1c) and might be considered to be derived from a "typical compromise" (Morris 1957) of the latter and BD Type I.

Vocalizations.—Several calls, most given by both sexes, were used during the final stages of pair formation. All were of low amplitude and were effective only for short-range communication. The brief, nasal "contact *Ernt*" call (Howe 1975) was the commonest and probably served as a pair-bond reinforcing signal and/or as a mechanism for maintaining contact during visual isolation. Often contact *Ernts* were repeated antiphonally for several seconds by members of a pair. Some observations suggest that such duetting might function to reduce the distance between birds. In one pair I watched for 2 hours, antiphonal contact *Ernts* were given frequently when the birds strayed apart while feeding. Usually one bird responded by flying in, landing close to the mate and resuming feeding activity. Several other distinct calls were given during pair formation (Howe 1972) but were less frequently heard than contact *Ernts*. The functions and physical characteristics of these calls will be reported elsewhere in detail.

Pair flights.—Among well established pairs I commonly saw the female initiate pair flights in which the male followed closely at several m or less. These flights could be short, simply from one side of a slough to the other, or long, possibly to the nesting area. Pair flights often took place shortly after a successful copulation and were at least sometimes preceded by an exchange of antiphonal contact *Ernt* calls (Howe 1972). Unlike the erratic aerial chases of early courtship (in which the male leads), pair flights usually followed a straight path, although the birds might circle back immediately before landing.

There appeared to be certain ritualized elements in the flight pattern of

females in pair flights. In contrast to normal flight, the wing beats were more rapid, the neck was somewhat extended, and the forward progress was unusually slow. These features indicate a possible relationship to the "Ceremonial Flight" of Northern Phalaropes, a circular flight performed by females (Tinbergen 1935). The ceremonial flight could be a ritualized form of a pair flight in which the male does not follow. If a male Wilson's Phalarope did not take flight with the female, she circled back and landed near him.

The functions of pair flights are not obvious. They possibly function as tests of pair bond strength during the critical period immediately before laying. They may also be a means of luring the male back to the area of the nest scrapes and communicating laying readiness. There are probably functional analogues in other shorebirds, such as the "Joint Flight" of Black-tailed Godwits, which Lind (1961) believed to be derived from the sexual pursuit. Such a derivation is not possible, however, in the phalaropes because the sex roles in aerial chases (sexual pursuits) and pair flights are reversed.

THE EGG-LAYING PERIOD

While the male was denuding nest scrapes, the female spent much time concealed in dense sedge sloughs. Presumably, at this stage of the nesting cycle, the female required additional food for egg production and consequently spent more time feeding. If the nest scrapes happened to be near the slough where the female was feeding, contact *Ernts* were occasionally exchanged by the members of the pair. Periodically the female walked out of the slough, calling with contact *Ernts* and joined her mate in a Scrape Ceremony at the scrape where he was working. Following the ceremony, she either walked or flew back to the slough. If she flew the male usually followed and copulation often took place. These visits to the scrape may have indicated the female's readiness to copulate. I did not determine whether females visited their mates when the nest area was far from the feeding slough.

Shortly before the first egg was laid, the male spent much time at the scrapes. When he left, he joined his mate in the slough where she was feeding. Since the birds did not defend areas away from the immediate vicinity of the scrapes, there was frequent mingling with other conspecifics at the feeding, loafing, and copulating areas. By this time the aggressive roles of the sexes had changed. Whereas earlier in pair formation the female aggressively defended her potential mate and the male rarely threatened, now the male threatened other conspecifics, especially courting females, and his mate rarely showed hostility. The only times I observed females exhibiting threat behavior during this stage of the breeding cycle were when copulations were interrupted by a nearby female or male. Höhn (1967) also noticed an in-

crease in male aggressive behavior later in the season but did not relate it to this specific period of the breeding cycle.

I watched 5 pairs extensively during the egg-laying period. Since I never observed laying of the first egg, however, I do not know whether the female visited more than one scrape before laying as Tinbergen (1935) observed in the Northern Phalarope. At several nests I was able to observe behavioral interactions between the sexes at the nest during and between the layings of the second, third, and fourth eggs. At these times I often saw the female walk out of the sedges of a nearby slough, proceed part of the way toward the nest and then return to the slough. Contact *Ernts* were exchanged between her and the male at the nest. As much as 2 hours before actual egg-laying time the female went to the nest, usually by an indirect route. She adopted the Scraping posture at the edge of the nest, which was being attended by the male, and a Scrape Ceremony would follow. Whether or not the ceremony was performed, the male then Crouch-Walked away and the female replaced him on the nest. During these visits to the nest the female performed nest-building movements and egg-laying sometimes occurred. Meanwhile the male remained about 2 m from the nest, preening, or else he flew to a nearby slough. These encounters differed from similar encounters during the nest-scrape preparation period in the longer period of time the female remained on the nest, performance of nest-building movements by the female, and the male's departure from the nest site. The use of the Scrape Ceremony during nest relief has been described in the Black-tailed Godwit (Lind 1961), Redshank (*Tringa totanus*) (Grosskopf 1959), Northern Phalarope (Tinbergen 1935), and other species.

When both members of a pair had been away from the nest during the egg-laying period, the male might return alone or both might return together. In the latter case, either sex could lead as the birds approached the nest, but the male was usually first to enter the nest (Table 2). The female then either walked away or replaced the male in the nest following the usual Scraping posture or Scrape Ceremony. Often both birds uttered rapid contact *Ernts* or variants thereof as they approached their nest. Other vocalizations audible only at very close range were sometimes given.

If an egg was not laid during the female's visit to the nest, she walked or flew back to the slough. During each of 5 actual layings I observed, the male flew to a nearby slough after being relieved at the nest. Females remained on the nest for an average of 13.8 min (range 10.5–17 min) at each laying and then flew directly to a slough. Before flying from the nest, each bird opened its bill slightly as if vocalizing.

Intervals between 2 consecutive layings were determined accurately in 3 cases: 25.5, 26.0, and 27.75 hours. All eggs were laid on consecutive days

TABLE 2

RELATIVE POSITIONS OF THE SEXES APPROACHING AND ENTERING THE NEST DURING THE EGG-LAYING PERIOD

| Sex Entering Nest | Position of Sexes Approaching | | | | Totals |
|-------------------|-------------------------------|--------|--------|--------------------|--------|
| | Male | Follow | Female | Female Follow Male | |
| Male | | 4 | | 6 | 10 |
| Female | | 1 | | 0 | 1 |
| Totals | | 5 | | 6 | 11 |

except once when at least 39 hours elapsed between layings. Höhn (1967) recorded 2 instances in which consecutive eggs were laid 2 days apart. The interval values I obtained compare with the following intervals for other shorebirds: Ruddy Turnstone (*Arenaria interpres*), 15–80 hours (Bergman 1946); Pectoral Sandpiper (*Calidris melanotos*), 24–29 hours (Parmelee, et al. 1967); Baird's Sandpiper (*C. bairdii*), 29–31 hours (Parmelee, et al. 1968); Sanderling (*C. alba*), 26–29 hours (Parmelee 1970); Dotterel (*Eudromias morinellus*), 39.9 hours (Pulliainen 1970).

The first egg of a clutch was deposited in a bare scrape. Shortly thereafter the male might begin lining the nest scrape with dead grass but the nest might also be ignored between the layings of the first and second eggs. Occurrence of the latter situation is based on periodic nest checks at which times the egg was cold and there was no evidence of lining. In gathering nest material the male faced away from the nest, tugged at dead matted grass stalks, and tossed them backward. This same behavior in the Black-tailed Godwit was termed "sideways throwing" by Lind (1961). It has also been widely reported among plovers and gulls. After tossing the grass backward, the male returned to the nest cup, avoiding the patches of thrown material. While sitting in the cup, he lined it by picking up and depositing the material in front of him or to one side. Several cup-shaping movements were performed and were apparently identical to those described by Lind (1961) for the Black-tailed Godwit. The lining was generally complete by the time the third egg was laid but building movements often continued into the first day or two of incubation.

Regular incubation behavior by the male generally began on the day the third egg was laid. On hot days, however, males would attend the eggs for several hours during earlier stages of the laying period.

BEHAVIOR OF FEMALES AFTER LAYING

After the fourth and final egg had been laid, the male returned to the nest to begin or continue incubation, and the behavioral mechanisms which

served to coordinate activities of the pair and maintain the bond ceased entirely. Observations were made on the subsequent behavior of 3 marked females. One remained in the immediate vicinity for 2 days and attempted to feed with her mate while he was off the nest between incubation bouts. Each time she approached within a few meters the male threatened her with a Head Forward Threat or Flying Threat. A second female also remained in her nest area for 2 days but did not associate with her former mate. Most of her activity was confined to a small portion of a large slough where she would utter sporadic contact *Ernts* at my approach and occasionally circle overhead, in the manner of a male flushed from a nest. Over the 2-day period she participated more and more in both short and long circling flights with other females. These flights were probably indicative of a developing flocking tendency since this bird completed laying on 4 June, the time at which post-breeding flocks of females began to accumulate on larger lakes.

I saw the third marked female in the company of a new male within several hours after completion of the clutch. Over a period of 5 min she gave 3 Head Forward Threats and 1 Flight Threat to another female. This was of particular interest since paired females rarely exhibited aggressive behavior. Although she soon became inattentive to the second male, the interaction suggested a return to behavior typical of the courtship phase. Tinbergen (1935) described a similar observation of Northern Phalaropes and suggested analogy with the performance of territorial behavior by certain bird species in the autumn. An alternative explanation, that at least some females attempt to pair successively with different males, seems more likely despite the opposing views of Höhn (1967) and Johns (1969). Recent studies (Raner 1972; Hilden and Vuolanto 1972) document the regular occurrence of serial polyandry in the Northern Phalarope.

Ovarian examinations of 10 females collected during the first week of June 1971 were made to determine the number of post-ovulatory follicles present. The results indicated that none of the females had laid more than one clutch, assuming that post-ovulatory follicles had not regressed beyond recognition. One bird, directing sexual displays toward a male when collected, showed possible signs of having laid eggs but the microscopic sections were inconclusive. These results, while not supporting the idea that Wilson's Phalaropes are polyandrous, do not rule out that possibility.

Female Wilson's Phalaropes were observed on the breeding grounds into the fourth week of June in North Dakota and some were still engaging in aerial chases, a feature of early pair formation, until close to the time of departure. Males off the nest between incubation bouts were often approached and followed in flight by females, which frequently adopted a hunched back posture with the neck retracted and head below the horizontal as in early

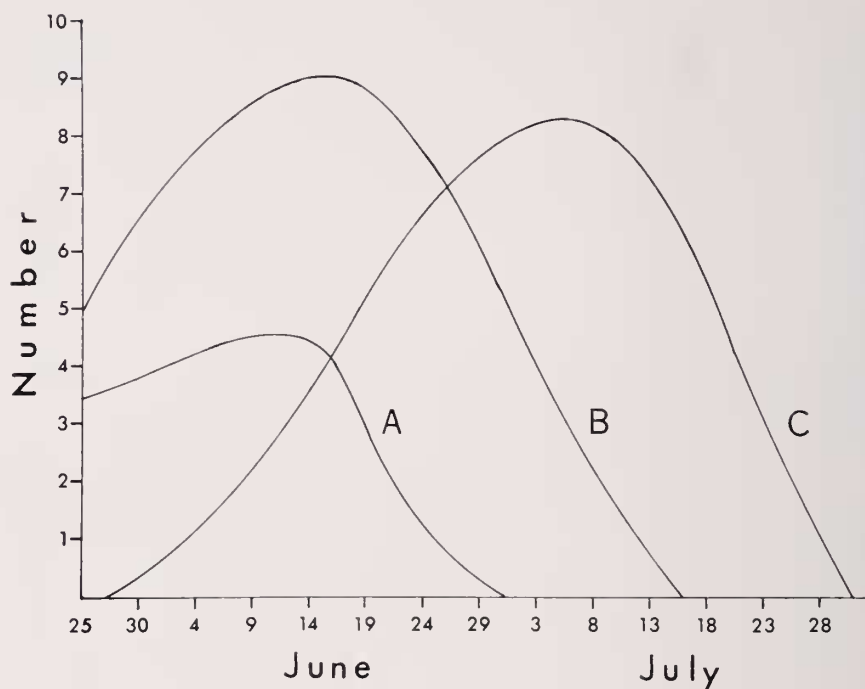


FIG. 4. Seasonal distribution of number of females observed on the main study area (A), number of clutches being incubated by males (B), and number of broods present (C). Data from 2 years were combined and averaged.

courtship (Howe 1975). Females even exhibited sexual interest in males attending broods and were especially attracted by males performing aerial distraction flights. I do not know whether any or all of these late females represented birds previously unsuccessful at obtaining mates. Their disappearance from the breeding grounds toward the latter part of June coincided with the time when most males were incubating and a few broods were already in evidence (Fig. 4).

DISCUSSION

Sex roles.—The pairing system of Wilson's Phalarope ranges from a period of intense competition for mates among females in social groupings to a period of pair isolation during which the behavior of males and females becomes geared toward attenuating intrapair hostility and coordinating sexual and nest-related activities. Although this general pattern of pair formation is shared by many species of birds, the reversal of sex roles in Wilson's

Phalaropes (and in other phalaropes) presents an additional facet with which the species must contend if successful breeding is to be achieved.

Female Wilson's Phalaropes, which are aggressive during early courtship, undergo a conspicuous reduction in aggressive tendency between the courtship and the egg-laying phases. During the same period the male acquires a complementary tendency to defend the pair bond against interference by conspecifics. Data presented in this paper indicate that the exchange of aggressive roles probably occurs about the time the potential nest sites have been selected and the male is preparing them for egg-laying. At this time the energy demand on the female for egg production may place severe constraints on her ability to continue active defense of the male. Hormonal changes accompanying egg production may inhibit aggressive expression as well. It therefore becomes adaptive for the male to take on the defending role, which includes defense of a small territory around the nest scrapes.

Female Wilson's Phalaropes are responsible for initiating nest-site searching and they participate as actively as the male during this process. They do not play a major role in nest-scraper preparation. In contrast, in most tringine sandpipers for which data are available, females play a less active role than males in nest-site searching and an equal or greater role in nest-scraper preparation. Males generally lead females in nest-site searching in the Black-tailed Godwit (Lind 1961), Redshank (Grosskopf 1959), Greenshank (*Tringa nebularia*) (Nethersole-Thompson 1951) and Willet (*Catoptrophorus semipalmatus*) (Vogt 1938). In the Greenshank (Nethersole-Thompson 1951) the female is apparently solely responsible for nest-scraper preparation. These tringines are apparently monogamous and the sexes share incubation. Sex roles in nest-site searching in the Northern Phalarope (Tinbergen 1935) follow the Wilson's Phalarope pattern of active female participation. Although the reason for the sex role differences in nest-site searching between Wilson's Phalaropes and tringines is not clear, it may be related to the fact that male phalaropes prepare the nests and therefore may require more precise cues from the female indicating readiness to lay.

Display homologies.—The displays used during the period of pair isolation by Wilson's Phalarope show much apparent homology with displays of other phalaropes but considerably less homology with displays of the more distantly related tringines. Chugging is probably homologous with the "Imposing posture" of Red and Northern phalaropes (Höhn 1971), in which the breast or neck feathers or both are fluffed and the head is held vertically. The Imposing posture has been observed as a female display during social courtship in both species and also as a female precopulatory display in the Northern Phalarope. No accompanying vocalizations have been reported.

Höhn points out the probable homologous relationships of the Head-Up

precopulatory display of the Red and Wilson's phalaropes, although the Head-Up is rarely given by Wilson's Phalarope from my experience (only 1 observation). The similar and more common PCU of Wilson's Phalarope has not been described for the other species. Interestingly, none of the phalaropes quivers the wings high above the back, a precopulatory display used by many tringines including the Redshank (Böcker 1958), Greenshank (Nethersole-Thompson 1951), Black-tailed Godwit (Lind 1961) and Willet (Vogt 1938).

No postures closely resembling the PCB's of Wilson's Phalarope (Fig. 1b, c, d) have been described for the other species. Höhn felt that Pushing in the Red Phalarope (Bengtson 1968), a display in which the bills are pointed down as a male and female make face-to-face contact prior to copulation, was homologous with the PCB. However, I consider the BD Type I (Fig. 3a) of Wilson's Phalarope the more likely homologue, and both are probably derived from displacement breast preening. No comparable display has been reported for the Northern Phalarope. The apparent absence of precopulatory displays with the head lowered in the Northern Phalarope may be a consequence of its preference for copulations in deep water. The only reference to a PCB-type display in tringines appears to be a Redshank display described by Böcker (1958), in which a rigid posture with head down and tail up is maintained for up to 1 min.

Displays related to egg-laying appear to be more highly developed in the Northern than in Wilson's phalarope. Tinbergen (1935) recorded a female Northern Phalarope performing several Ceremonial Flights before laying, with the male following her in each. The possible relationships between the Ceremonial Flight and the pair flights of Wilson's Phalarope were discussed above. After laying, the female and male Northern Phalaropes engaged in up to 20 Scrape Ceremonies, including Ground-Pecking (apparently identical to the display of Wilson's Phalarope, Fig. 1c), and the male also made several nest-building movements. This process was repeated at every laying by the pair he had under observation. By contrast, female Wilson's Phalaropes do not perform Ceremonial Flights, and after laying they fly directly from the nest to a nearby slough. The male does not remain at the nest while the egg is being laid. Possibly more mutual display is necessary to reinforce sexual recognition in the Northern Phalarope, which is less sexually dimorphic in plumage than Wilson's.

Polyandry.—The question of whether polyandry is a major force in Wilson's Phalarope breeding biology, or whether it exists at all, remains unresolved, although some investigators have considered Wilson's Phalaropes to be polyandrous. The history of these interpretations of observational data is reviewed by Höhn (1967), who concluded that no good evidence exists for

polyandry in the species. Johns (1969) agreed with this conclusion. Since that time Raner (1972) and Hilden and Vuolanto (1972) have found cases of serial polyandry in Northern Phalaropes. These were the first convincing published records of true polyandry in any scolopacid (*sensu* Jehl 1968). Raner (1972) also presented evidence of polyandry in the Spotted Redshank (*Tringa erythropus*). More recently a partially polyandrous system has been discovered in the Spotted Sandpiper (*Actitis macularia*) in 2 separate studies (Oring and Knudsen 1973, Hays 1973). Female Spotted Sandpipers occasionally incubate, however, suggesting a more flexible system than in Northern Phalaropes. Two other recently published studies describe highly flexible mating systems in 2 species of plovers (Charadriidae). Both the Mountain Plover (*Charadrius montanus*) and Dotterel show a range of systems including monogamy, polygyny, and polyandry (Graul 1974, and Nethersole-Thompson 1973). These studies make it clear that the possibility of serial polyandry in Wilson's Phalarope must be seriously considered despite the inconclusive evidence presented in this paper.

The ovarian examinations I made of breeding Wilson's Phalaropes did not show evidence of multiple clutches. However, the observation reported in this study of a female exhibiting sexual interest in a male shortly after laying a clutch for another male is suggestive of a tendency toward serial polyandry. An additional indirect line of evidence lends further support to this possibility. Lack (1968) pointed out that several species of scolopacid sandpipers lay unusually light eggs in proportion to body weight. Three of these species, Temminck's Stint (*Calidris temminckii*) (Hilden 1965), the Sanderling (Parmelee and Payne 1973), and the Northern Phalarope (Hilden and Vuolanto 1972), have been proven to lay multiple clutches. The latter authors point out that the Common Snipe also lays relatively small eggs and is known to produce frequent multiple clutches. Reducing clutch weight may be viewed as an adaptation for reducing energy demands on females which often lay more than one clutch (Parmelee and Payne 1973). Both Wilson's and Red Phalaropes lay proportionately small eggs, suggesting that multiple clutches may also occur in these species.

The mechanism by which a polyandrous mating system can evolve has long been unexplained. Recently, however, Nethersole-Thompson (1973) and Graul (1974) have independently advanced similar explanations for the evolution of polyandry in Dotterels and Mountain Plovers, respectively. The theoretical arguments have been especially well developed by Graul (1974). According to the latter, male Mountain Plovers in habitats experiencing severe fluctuations in food supply may be capable of raising a brood alone while the females, due to the energy depletion resulting from egg-laying, may be incapable of so doing. This situation commits the male

to increased parental responsibilities and leaves him vulnerable to desertion by the female. During favorable periods of food availability, the female may be able to recover enough energy reserves to lay a clutch for a second male. Graul discusses various ramifications of this idea.

This explanation may be applicable to phalaropes as well. Phalaropes occupy a unique feeding niche among shorebirds, often feeding on minute invertebrates taken while the birds are swimming in deep water. Although evidence is wanting, this feeding regime may experience fluctuations in food availability similar to those experienced by Mountain Plovers in arid grassland habitats. Detailed investigation of the phalarope feeding niche is certainly warranted and could provide the evidence necessary to explain polyandry in the Northern Phalarope, and possibly in other phalaropes.

SUMMARY

The behavior patterns of male and female Wilson's Phalaropes during the later stages of pair formation and the paired period are described. Females initiate nest-site searching behavior by leading males away from shores of sloughs into drier, grassy areas. During searching behavior each sex is equally likely to lead the other or both may wander in separate directions. Displays during this period are described and illustrated. The male alone prepares several nest scrapes for egg-laying by removing old and new grass, leaving a bare cup. A single observation of a male defending an area around the nest scrapes is the only evidence of territorial behavior by males observed in the entire study.

Pre-copulatory behavior is described and an attempt is made to quantify display sequences leading to copulation. There are no post-copulatory displays. The average duration of copulations is 46.5 sec. Only 1 of 51 observed copulations took place while swimming.

Paired birds and birds in the final stages of pair formation exhibit several behavior patterns which seem to function as aggression-reducing mechanisms. Most conspicuous are periods of ritualized preening and performance of Bill-Down displays. Flights in which the female leads the male are frequent at this time and may indicate laying readiness.

The female lays eggs in one of the prepared scrapes. The male is usually at the nest when she arrives and she replaces him. Usually the male flies to a slough where he is joined by the female after egg-laying, which lasts about 14 min. A clutch of 4 was usually completed in 4 days with an average interval between eggs of 26.4 hours. The male begins lining the nest with dead grass shortly after the first egg has been laid. Incubation is solely by the male and usually begins on a regular basis after the third egg is laid.

The male is hostile toward his mate soon after the last egg is laid and the bond is essentially dissolved at this time. There was one observation of a female directing sexual behavior toward another male after completing a clutch, but microscopic analysis of ovaries from collected birds did not show evidence of multiple clutches.

The motivational and evolutionary relationships among several displays are discussed and possible homologies with displays of other phalaropes investigated. The evidence for polyandry is examined in light of recent studies and one possible mechanism for its evolution is presented.

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